

Jaguar and Puma Activity Patterns and Predator-Prey Interactions in Four Brazilian Biomes

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ABSTRACT

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) coexist throughout the Neotropics. Using camera trapping in four Brazilian biomes, we compare the daily activity patterns of the jaguar and puma, and their relationships with their main prey species. We used a kernel density method to quantify daily activity patterns and to investigate overlap between these predators and their main prey. Both cats showed intensive nocturnal and crepuscular activity (0.69 and 0.14 kernel density, respectively, for jaguars; 0.68 and 0.19 kernel density, respectively, for pumas). Only in the Pantanal did we observe a pattern of concentrated diurnal activity for both species. We found little temporal segregation between jaguars and pumas, as they showed similar activity patterns with high coefficients of overlapping (average $\Delta_1 = 0.86$; SE = 0.15). We also observed a significant overlap between the activity patterns of the predators and their main prey species, suggesting that both predators adjust their activity to reduce their foraging energy expenditure. Our findings suggest that temporal partitioning is probably not a generalized mechanism of coexistence between jaguars and pumas; instead, the partitioning of habitat/space use and food resources may play a larger role in mediating top predator coexistence. Knowledge about these behavior aspects is crucial to elucidating the factors that enable coexistence of jaguars and pumas. Furthermore, an understanding of their respective activity periods is relevant to management and associated research efforts.

Abstract in Portuguese is available in the online version of this article.

Key words: camera trapping; coefficient of overlapping; kernel density estimator; *Panthera onca*; predator coexistence; *Puma concolor*; temporal partitioning

COEXISTENCE OF SIMILAR SPECIES IS DIFFICULT TO EXPLAIN IF TWO SPECIES share very similar niches, as the competitive exclusion principle predicts the extinction of the inferior competitor (Hutchinson 1978, Soberon 2007). Alternatively, competition can drive niche differentiation by which competing species pursue dissimilar patterns of resource use. Therefore, coexistence is acquired through the segregation of ecological niches (Hutchinson 1978). For sympatric carnivores, such as large cats, it has been suggested that coexistence could be mediated by ecological and behavioral factors that include different habitat use, temporal partitioning (Palomares *et al.* 1996, Durant 1998), and partitioning of resources, such as the capture of distinct prey species of different sizes, to reduce competition (Taber *et al.* 1997, Karanth & Sunquist 2000, Jácomo *et al.* 2004).

The jaguar (*Panthera onca*) and the puma (*Puma concolor*), the largest terrestrial predators that coexist throughout the Neotropics, represent suitable subjects for studying coexistence strategies due to their similar ecological requirements. These two predators constitute a large mammalian predator guild that has a significant influence on the structure and functionality of the ecosystems, controlling the number of herbivores and consequently decreasing

the pressure that they exert on plants (Miller *et al.* 2001). Their loss may result in changes in community structure, as has been found in other systems that have lost their top terrestrial predators (Diamond 2001, Terborgh *et al.* 2001, Terborgh & Estes 2010). Both cats exploit the same environmental resources and have similar life strategies and resource use (Root 1967).

The jaguar is generally considered to be more specialized than the puma; it prefers dense habitats (forest and scrublands as opposed to open grasslands and swamps) close to water (Sollmann *et al.* 2012) and avoids anthropogenic habitats (Cullen 2006), whereas the puma is more adaptable to a wider spectrum of habitats, and is less dependent on water bodies (Iriarte *et al.* 1990, Sollmann *et al.* 2012). Jaguars and pumas are considered generalist predators; they feed on a wide range of prey species, with peccaries, deer, large caviomorph rodents, and armadillos comprising the bulk of their diets (Oliveira 2002). Both species are known to vary their prey selection across different biomes (Astete *et al.* 2008). Due to greater body mass, jaguars are thought to depend on larger prey (Emmons 1987) to a greater extent than pumas, which often select smaller prey species when occurring sympatrically with jaguars, presumably to minimize competition (Iriarte *et al.* 1990, Taber *et al.* 1997, Scognamiglio *et al.* 2003, Haines 2006). Nevertheless, other studies have shown high dietary niche overlap (Núñez *et al.* 2000, Haines

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2006). Others have suggested that co-occurring jaguars and pumas avoid encounters using different habitats in different ways (Polisar *et al.* 2003, Scognamillo *et al.* 2003, Harmsen *et al.* 2009, Sollmann *et al.* 2012). The activity patterns of both species could also be adjusted to those of their main prey species to reduce energy expenditure (Iriarte *et al.* 1990, Romero-Muñoz *et al.* 2010). This can include an adaptation to the daily activity patterns of prey or an alternative strategy that consists of attacking non-vigilant animals, which can increase capture success, as the prey tends to react more slowly.

The objective of this study was to compare the activity patterns of jaguars, pumas, and their main prey species, using camera trapping, in four study areas located in different Brazilian biomes, to answer three questions: (1) Do pumas and jaguars show temporal activity avoidance, which would suggest a strategy of reducing interference competition and allowing for coexistence? (2) Are there significant differences in the temporal activity of both species among biomes? (3) Is there any evidence that jaguar and/or puma activity patterns overlap with those of their main prey? Knowledge about these aspects of behavior is crucial to comprehending the factors that enable the coexistence of jaguars and pumas and to allow a better understanding of their ecological requirements (Núñez *et al.* 2000, Scognamillo *et al.* 2003).

METHODS

STUDY AREAS.—We conducted our study in two protected areas and two private ranches located in distinct Brazilian biomes (Fig. S1). Emas National Park (ENP, 132,000 ha) is situated in central Brazil in the extreme southwest of Goiás State (18°19'59" S, 52°45'00" W). It protects large tracts of grassland plain, and small patches of shrub fields (cerrado *sensu stricto*), marshes, and riparian forest, and it is widely known for its rich and abundant grassland fauna (Redford 1983).

Santa Fé Ranch (SFR, 09°34'16" S, 50°21'45" W) is a private property situated in the cerrado/Amazon ecotone in the southeast of Pará State. The SFR is a 65,000 ha beef cattle ranch, which includes a 30,000 ha protected reserve, composed of secondary growth tropical rain forest that stretches beyond the farm boundaries (Negroes *et al.* 2010). Pastures occupy 35 percent of the ranch. The ranch is situated in the so-called 'arc of deforestation', a region along the southern border of the Amazon undergoing strong anthropogenic impacts (Morton *et al.* 2006).

Serra da Capivara National Park (SCNP, 8° 26'50" S, 42° 19' 47" W) is situated in the south of Piauí State, in the semi-arid Caatinga biome of northeastern Brazil, with an area of 129,140 ha that is predominantly covered by 6–10 m tall shrubby vegetation (Emperaire 1984). Refúgio Ecológico Caiman (REC, 19°57'39" S, 56°18'20" W) is predominantly a cattle ranch covering an area of 53,000 ha, 7000 ha of which is protected. Located in the Pantanal of Mato Grosso do Sul State, the vegetation of REC consists of a mosaic of floodplains, grasslands, savannas, scrub savannas, arboreal savannas, forests of riparian vegetation, and man-made pastures with artificial ponds as a water source for cattle and wildlife.

CAMERA-TRAPPING.—We used data from camera trap surveys to assess the activity patterns of jaguars and pumas and their potential prey species. We deployed cameras at 119 stations from March to June 2008 and 110 stations from March to June 2010 in ENP, 34 stations from February to November 2007 in SFR, 71 stations from September 2009 to January 2010 in SCNP, and 142 stations from January 2002 to January 2005 in REC, in a grid spaced approximately 2–3 km apart (Table 1). Each station consisted of two passive infrared cameras facing each other, except for REC surveys where each station consisted of one camera, and were placed along dirt roads or trails, approximately 40–50 cm above the ground. We used two camera types: Leaf-River C1-BU (Vibrashine Inc.[®], Taylorsville, U.S.A.) and Camtrakker (CamTrakker[®], Watkinsville, GA). All stations were checked at 10–15 d intervals to change film and batteries if necessary during surveys. Cameras were programmed to operate for 24 h/d in shady sites and only during the night in sites exposed to direct sunlight, as cameras can easily be triggered by sunlight in open areas. Only data from the former were used to study the activity patterns of our focal species (Table 1).

PREY SPECIES.—To compare the activity patterns of predators and their respective prey species, we selected the most representative prey in each predator's diet in each biome, as reported by previous studies (Table S1), with a few exceptions as described below. For the jaguar in SCNP, the yellow armadillo (*Euphractus sexcinctus*) was the species most often consumed, with an occurrence of 55 percent in scat samples (Jaguar Conservation Fund, unpubl. data). The low number of photographic records for this species ($N = 5$), however, did not allow robust analysis. Instead, we chose the lesser anteater (*Tamandua tetradactyla*), which was the second most consumed prey species with a frequency of occurrence of 22.4 percent in the analyzed scats and represented 22 percent of the biomass consumed (Jaguar Conservation Fund, unpubl. data). In the SFR, the family Tayassuidae, together with livestock and lesser anteater represented the main prey species for jaguars (17%, 14%, and 14% relative occurrence, respectively) (Jaguar Conservation Fund, unpubl. data). Due to the absence of photographic records for the lesser anteater and livestock, we chose the Tayassuidae family to represent the main prey species in this area. Due to a lack of information about the feeding habits of pumas in SFR, analysis on this species and its main prey was not carried out for this region.

STATISTICAL ANALYSIS.—All cameras recorded the time and date of each photograph and we compiled this information for jaguars, pumas, and prey species (Table 2). To avoid autocorrelation, we only used photographs of the same species from the same camera that had been obtained more than 1 h apart, except when it was possible to identify distinct individuals (Silveira *et al.* 2003, Linkie & Ridout 2011). In that case, if there were two consecutive visits to the same camera by two different individuals, these were considered as two independent captures. Activity of jaguars, pumas, and their prey species were classified into four categories: diurnal (activity predominantly between 1 h after the sunrise and

TABLE 1. Camera trapping periods, number of trap stations (the number of 24 h trap stations and the respective trapping days are in parentheses), and trapping days for several trapping campaigns in our four study areas in Brazil.

Biome	Study area	Period of Surveys	Trap stations	Trapping days
Cerrado	ENP	March–June/2008	119 (96)	9639 (7872)
		March–June/2010	110 (17)	6930 (1037)
Ecótone	SFR	February–November/2007	34 (34)	2176
Caatinga	SCNP	September/2009–January/2010	71 (71)	8804
Pantanal	REC	January/2002–January/2005	142 (142)	7100

ENP – Emas National Park; SFR – Santa Fé Ranch; SCNP – Serra da Capivara National Park; REC – Refúgio Ecológico Caiman.

TABLE 2. Number of records and capture rate (per 100 trap-days) for jaguars, pumas and their main prey species in our four study areas.

Species	Study area			
	REC	ENP	SCNP	SFR
Jaguar	111 (4.7)	50 (2.3)	170 (3.3)	89 (7.3)
Puma	96 (3.9)	37 (2.0)	112 (2.9)	81 (6.6)
Giant anteater	105 (4.5)	110 (3.0)	–	1 (4.5)
Collared peccary	171 (8.0)	7 (1.5)	39 (4.0)	33 (4.3)
Capybara	105 (8.2)	–	–	7 (2.7)
Lesser Anteater	11 (2.0)	2 (1.3)	27 (1.9)	–
Armadillos	37 (4.1)	49 (2.4)	115 (2.9)	16 (2.8)

ENP – Emas National Park; SFR – Santa Fé Ranch; SCNP – Serra da Capivara National Park; REC – Refúgio Ecológico Caiman.

1 h before the sunset); nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise); cathemeral (peaks of activity through the diurnal and nocturnal period) and crepuscular. The last category was defined as events that occurred 1 h before and after sunrise and sunset. We determined the exact time of sunset and sunrise using the software Moonrise 3.5, which used the time of day, date and coordinates of each record. To avoid incorrect definitions of species activity patterns, times of capture were converted to solar time. As solar time is based on the position of the sun in the sky, it compensates for the local time zone and daylight savings, making comparison between seasons and study areas possible. To quantify the overlap between the activity patterns of jaguars, pumas, and their prey species, we used the two-step approach developed by Ridout and Linkie (2009). The first step consists of estimating each activity pattern separately using kernel density estimates which, instead of grouping pictures into discrete time categories, treats them as random samples from an underlying continuous distribution. In this phase, we calculated the proportion of activity for each period (day, night, cathemeral, and crepuscular) by integrating the areas under the activity curve for each respective period that corresponded to the probability of observing the animal during that time period. For the second step, we calculated the coefficient of overlapping (Δ), which varies from 0 (no overlap), to 1 (complete

overlap) (Ridout & Linkie 2009). The authors present several alternative methods for calculating the coefficient of overlapping. Here, we used their estimator Δ_1 which is the most suitable for small sample sizes (Ridout & Linkie 2009). This coefficient is defined as: $\Delta_1 = \int_0^1 \min\{\hat{f}(t), \hat{g}(t)\} dt$, where $\hat{f}\{t\}$ and $\hat{g}\{t\}$ are the two activity functions of time t being compared.

Statistical analyses were implemented in the software R 2.13.0 (R Development Core Team 2011) using an adaptation of the scripts developed by Linkie and Ridout (2011) available at <http://www.kent.ac.uk/ims/personal/msr/overlap.html>. We calculated the 95 percent confidence intervals for Δ as percentile intervals from 500 bootstrap samples. We made comparisons among species in the same study area and for the same species among different study areas.

As each study area presented different sampling periods (years and seasons), we investigated if there were significant differences in the activity patterns of focal among years and/or seasons to verify if it was adequate to combine data within a single analysis of activity patterns. Considering the proximity of all study areas to the Equator, there are only small differences in terms of sunlight hours throughout the year (approximately 1 h). We produced a boxplot of the daily sunlight hours during our study periods for all study areas to check for potential variation. As the data was normally distributed, we applied a normal one-way ANOVA to verify the existence of significant differences in the solar period among the four study areas. We used the coefficient of overlapping (Δ) to quantify differences in the activity patterns of our focal species between years and/or seasons in each study area.

RESULTS

We obtained a total of 1608 independent records of jaguars, pumas, and their main prey species. The highest number of the records for focal species was obtained in REC, whereas for jaguar and puma, the highest number of records was obtained in SCNP (Table 2).

In the analyses to investigate the possibility to combine data across years and seasons we observed only small and insignificant variations in activity patterns. The one-way ANOVA revealed no significant differences in the sunlight period between the four areas during the studies ($F_{3,36} = 1.347$, $P = 0.274$). For the

TABLE 3. Coefficient of overlapping (Δ_1) of daily activity patterns of jaguars and pumas among four study areas in different Brazilian biomes (95% bootstrap confidence intervals are in parentheses).

	Overlap value (Kernel density - Δ_1)		
	SFR	REC	SCNP
Jaguar			
ENP	0.62 (0.49–0.74)	0.78 (0.66–0.83)	0.85 (0.68–0.88)
SCNP	0.64 (0.55–0.70)	0.75 (0.60–0.78)	–
REC	0.68 (0.56–0.80)	–	–
Puma			
ENP	0.85 (0.68–0.91)	0.85 (0.68–0.91)	0.81 (0.59–0.87)
SCNP	0.68 (0.58–0.76)	0.82 (0.68–0.88)	–
REC	0.79 (0.68–0.86)	–	–

ENP – Emas National Park; SFR – Santa Fé Ranch; SCNP – Serra da Capivara National Park; REC – Refúgio Ecológico Caiman.

2 years of our study, in ENP, we obtained a coefficient of overlapping (Δ_1) of 0.83 for jaguar and 0.78 for puma. For SFR we compared the data from 2006 and 2007 and we also obtained a suitable concordance between both years (0.93 for jaguar and 0.78 for puma). Regarding SCNP, we compared the data from the dry and wet season (sampling was performed from September 2009 till January 2010) and we obtained a Δ_1 of 0.86 for jaguar and 0.82 for puma. Finally, for REC between years, we obtained an average Δ_1 of 0.77 for jaguars and of 0.73 for pumas, and between seasons (dry and wet) an average Δ_1 of 0.73 for jaguar and 0.85 for puma. These results indicate that for all study areas was acceptable to combine data across years and seasons, as there were no apparent changes in activity patterns.

ACTIVITY PATTERNS.—Overall, jaguars and pumas showed intensive nocturnal and crepuscular activity (0.69 and 0.14 kernel density, respectively, for jaguars and 0.68 and 0.19 kernel density,

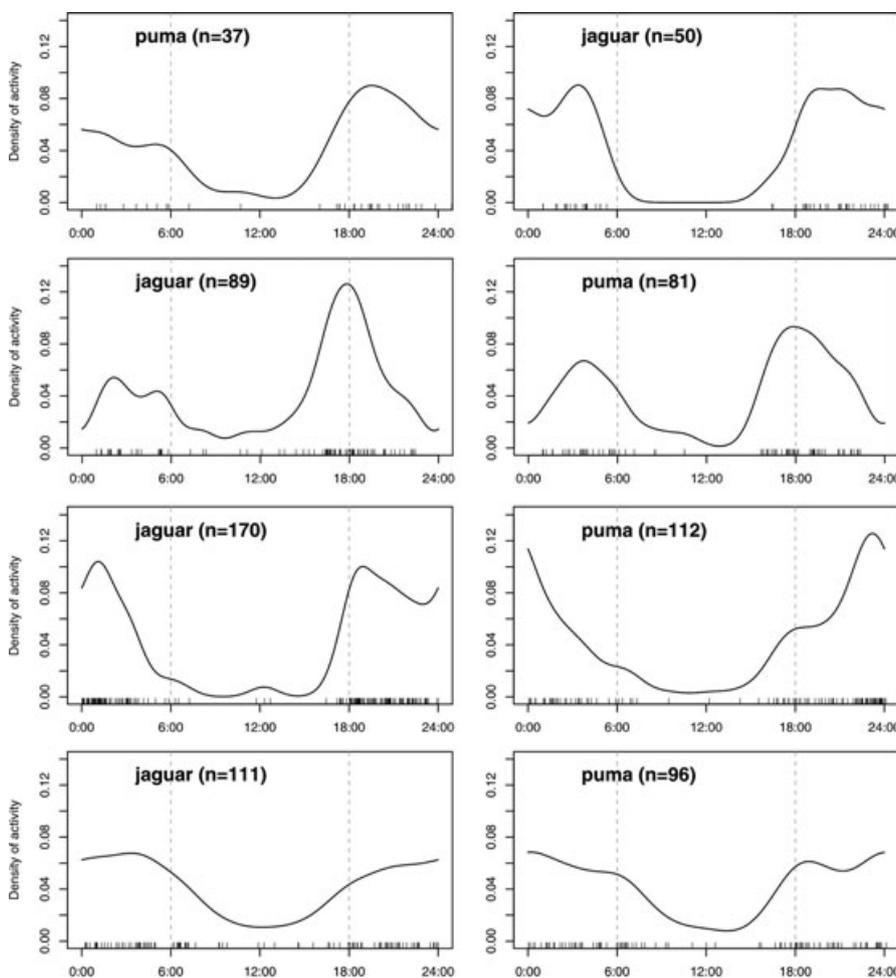


FIGURE 1. Kernel densities of jaguar and puma activity (solid lines) in Emas National Park (row 1, top), Santa Fé Ranch (row 2), Serra da Capivara National Park (row 3) and Refúgio Ecológico Caiman (row 4). Individual records are shown as short vertical lines above the x-axis. The grey dashed lines represent the approximate time of sunrise and sunset.

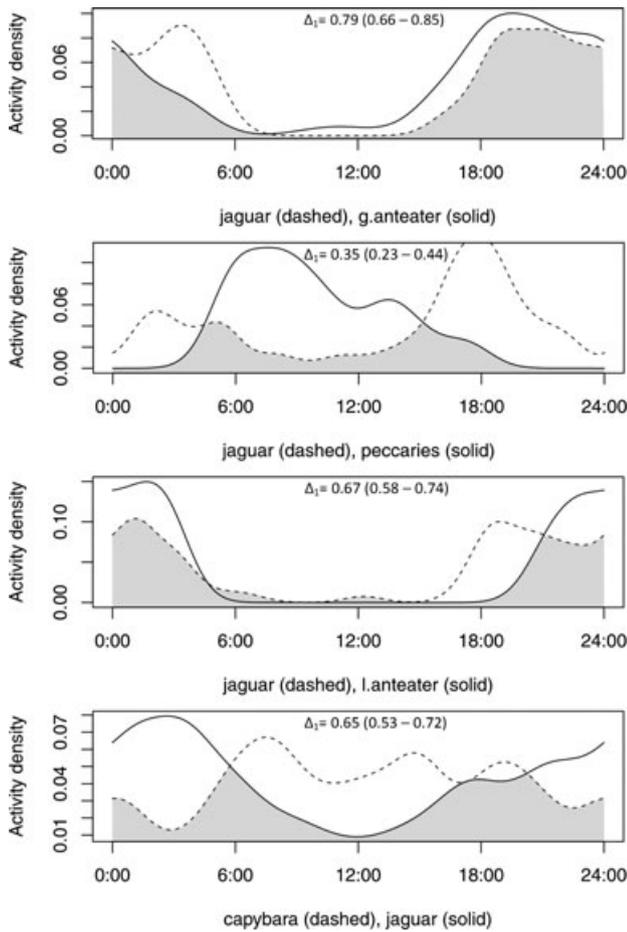


FIGURE 2. Coefficient of overlapping of daily activity patterns between the jaguar and its main preys species in four study areas in Brazil; Emas National Park (row 1, top), sample sizes: jaguar ($N = 50$), g. anteater ($N = 110$); Santa Fé Ranch (row 2), sample sizes: jaguar ($N = 89$), peccaries ($N = 33$); Serra da Capivara National Park (row 3), sample sizes: jaguar ($N = 170$), l. anteater ($N = 27$); and Refúgio Ecológico Caiman (row 4), samples sizes: jaguar (111), capybara (105). Overlap is represented by the shaded area.

respectively, for pumas). The activity patterns of jaguars were similar among all study areas, with an average Δ_1 of 0.73 (SE = 0.05) (Table 3). Activity patterns were most similar between ENP and SCNP ($\Delta_1 = 0.85$; SE = 0.03), where the species showed very little diurnal activity (Fig. 1; Table 3). The lowest average overlap index with other areas was observed for SFR ($\Delta_1 = 0.65$; SE = 0.03). Here, although predominately nocturnal, the species had activity peaks mostly around dusk (Fig. 1). In the REC, although most activity was also nocturnal (0.74 of kernel density), the species exhibited a more diurnal pattern compared to the other study areas (0.18 of kernel density) (Fig. 1). The average observed activity overlap with other areas was 0.74 (SE = 0.04).

Puma activity patterns were very similar among study areas, with an average overlap coefficient of 0.80 (SE = 0.03) (Table 3). We observed the most diurnal activity in REC (0.15 of kernel density). In SCNP, almost no diurnal activity was observed

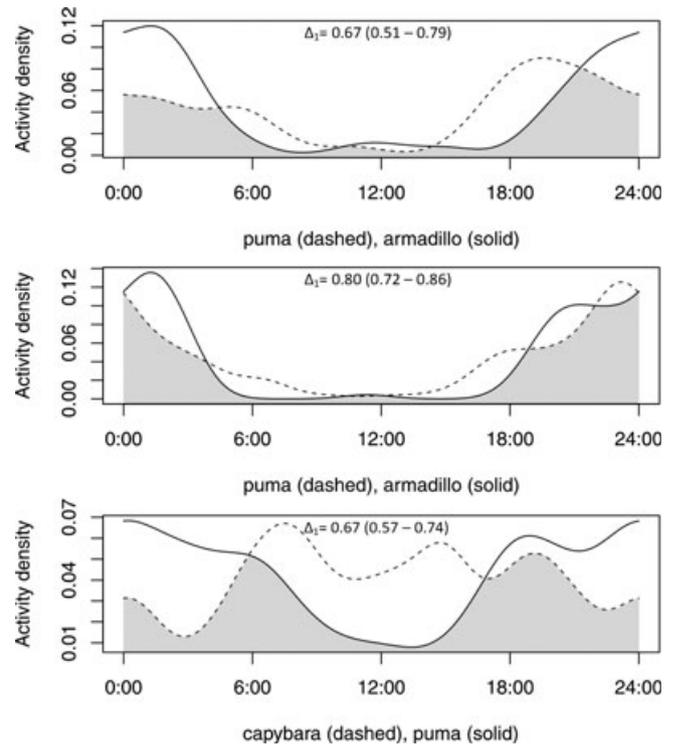


FIGURE 3. Coefficient of overlapping between the puma and its main prey species in four study areas in Brazil; Emas National Park (row 1, top), samples size: puma ($N = 37$), armadillo (49); Serra da Capivara National Park (row 2), samples size: puma ($N = 112$), armadillo (115); and Refúgio Ecológico Caiman (row 3), samples size: puma ($N = 96$), capybara (105). Overlap is value represented by the shaded area.

(Fig. 1) and here, also, we observed the lowest average coefficient of overlapping with other study areas ($\Delta_1 = 0.77$; SE = 0.05). The comparison of daily activity patterns between jaguars and pumas showed high and very similar Δ_1 values in all study areas (average $\Delta_1 = 0.86$; SE = 0.15). The lowest Δ_1 value was observed in SCNP (0.82), followed by ENP (0.83) and SFR (0.85). The highest coefficient of overlapping was observed in REC (0.95).

Considering prey species, the lesser anteater and armadillo species were nocturnal (1.00 and 0.90 of kernel density, respectively), both having activity peaks at dawn and dusk (Figs. 2 and 3). The giant anteater (*Mirmecophaga tridactyla*) was also predominantly nocturnal (0.59 of kernel density), showing activity peaks during the first half of the night. Capybara (*Hydrochoerus hydrochaeris*) activity was cathemeral with some activity peaks during the day and at the beginning of the night (Figs. 2 and 3). Peccaries were the only prey item that showed predominantly diurnal activity with 0.68 kernel probability of being active during the day.

We observed an average Δ_1 of 0.62 (SE = 0.14) between jaguars and their main prey species. The highest activity concordance was observed for the giant anteater in ENP and the lowest with peccaries in SFR (Fig. 2). For the puma, the average Δ_1 across its prey species was 0.69 (SE = 0.08), varying between

0.60 for armadillos in ENP and 0.80 for nine-band armadillos in SCNP (Fig. 3).

DISCUSSION

DAILY ACTIVITY PATTERNS.—Adaptation of activity patterns has been proposed as a mechanism to minimize interference competition among foragers, particularly the existence of diel differences in activity (Gotelli & Graves 1996, Durant 1998). Temporal partitioning, however, is rarely considered as the main mechanism that potential competitors use to reduce competition; it is more common that animals segregate by food or habitat use (Schoener 1974). In this study, we did not observe strong temporal partitioning between jaguars and pumas. Both species showed similar nocturnal and crepuscular activity with high overlap coefficients throughout all study sites. These observations concur with the results of studies conducted in the Venezuelan llanos (Scognamillo *et al.* 2003) and in the Belizean rain forest (Harmsen *et al.* 2009).

Moreover, in the Belizean rain forest, jaguar and puma activity was predominantly nocturnal (Harmsen *et al.* 2009), with a pattern very similar to our results from SCNP. Although in ENP and SFR both cats showed mostly nocturnal activity with activity peaks between 1800 and 0400 hours, the puma exhibited more diurnal activity in ENP, whereas the jaguar presented diurnal activity only in SFR. These findings are similar to results obtained in the Venezuelan llanos (Scognamillo *et al.* 2003). In REC, both cats showed higher diurnal activity than in other biomes. This behavior may be associated with the activity period of capybara, their main prey species, which present activity peaks during the day and the first hours of the night.

A clear influence of prey species in the temporal segregation of the predators has been observed for other sympatric carnivores, such as tigers and leopards in India, suggesting that the activity patterns of these predators could be more linked to prey activities than avoidance of each other (Karanth & Sunquist 2000). Contrarily, in the Paraguayan Chaco (Taber *et al.* 1997) and in southern Bolivia (Romero-Muñoz *et al.* 2010), jaguars and pumas showed distinct activity patterns, suggesting that the puma avoided the jaguar's main activity period. In those studies, the predators did not follow the daily activity schedules of any one particular prey species; instead, they appeared to segregate their activity patterns to avoid each other (Romero-Muñoz *et al.* 2010).

Some authors have suggested that the activity patterns of jaguars and pumas are determined by the daily activity patterns of their prey species (Emmons 1987, Núñez *et al.* 2000, Scognamillo *et al.* 2003, Harmsen *et al.* 2009). In fact, these studies have found a significant overlap in activity between both predators and their main prey, as observed in our study, lending support to the opportunistic hunting theory, which states that predators adjust their activity to reduce foraging energy expenditure (Sunquist & Sunquist 1989). For example, in REC, jaguars and pumas have a similar diet, based on diurnal capybara, and similar daily activity patterns. Here, the high abundance of capybaras and differing size selection of capybaras by the two predators—jaguars prefer

large capybaras (> 15 kg) (Azevedo & Murray 2007), whereas puma hunt mostly medium-sized ones (1–15 kg) (Emmons 1987, Iriarte *et al.* 1990, Scognamillo *et al.* 2003)—might facilitate their coexistence (Azevedo & Murray 2007).

For jaguars, overlap in the species' activity patterns with that of its main prey species was typical of all study areas, except in SFR where there was low activity overlap with peccaries. Hunting may occur when the prey species are not active and probably more vulnerable than other periods (Sunquist & Sunquist 1989), thereby reducing the risk of injury to the predator (Azevedo & Murray 2007). Due to the jaguar's generalist feeding behavior, however, these results could also imply that this predator allocates activity to other periods when alternative prey species are active (Harmsen *et al.* 2011). While peccaries are the most important prey species for the jaguar in this area, lesser anteaters and cattle also occur significantly in their diet. The low number of photographic records for these latter species limited our analysis to the Tayassuidae. As a result, we may have failed to detect potential overlap in activity patterns with other prey species.

In conclusion, camera trapping allowed us to provide a general overview of the temporal interactions between jaguars, pumas, and their prey in different environments. Temporal partitioning is probably not a generalized mechanism of coexistence between jaguars and pumas, and partitioning of habitat/space and food resource might play a larger role in mediating top predator coexistence in these areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of Brazilian biomes showing the study areas.

TABLE S1. *Main prey species cited in the literature for the jaguar and puma in our four study areas in Brazil.*

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